

STUDIES INVOLVING SUSTAINED TREATMENT OF MAIZE WITH GIBBERELIC ACID II: RESPONSES OF PLANTS CARRYING CERTAIN TASSEL-MODIFYING GENES*

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ABSTRACT

Plants containing each one of seven different tassel-modifying genes were treated with Gibberellic Acid-distilled water mixtures every three days throughout the growing season until tassel emergence. GA was found to suppress expression of *ramosa-1* (*ra*₁). Tassel-seeds 2 (*ts*₂), 5 (*Ts*₅) and 6 (*Ts*₆), Tunicate (*Tu*) and Vestigial glume (*Vg*) were all modified, but not so much that they could not be recognized. The recessive male-sterile 1 (*ms*₁) remained male-sterile. An explanation of certain elongation patterns in these plants is tentatively made, which points toward the idea that GA depends at least in part on the presence of auxin (IAA) for its effects. NORTON H. NICKERSON, Missouri Botanical Garden, 2315 Tower Grove Ave., St. Louis 10, Missouri.

INTRODUCTION

Phinney (1956) showed that *dwarf-1*, a recessive maize mutant, responded to Gibberellic Acid (hereinafter called GA) in such a way as to become phenotypically normal with a total amount of 60 micrograms of GA applied regularly during the growing season. Recently (Nickerson, 1960a) it has been shown that the dominant maize genes Corn-grass (*Cg*) and Teopod (*Tp*) likewise respond to sustained GA treatments in a like manner, becoming essentially normal in phenotype. It has also been shown previously (Nickerson, 1959; Nickerson and Embler, 1960) that normal maize plants respond to sustained treatment with GA in several characteristic ways. Inasmuch as some of the growth manifestations noted under such GA treatment resembled some known tassel mutants, it was decided to grow obtainable seed of a series of tassel mutants previously studied (Nickerson and Dale, 1955) and subject them to various strengths of GA treatment throughout their growing seasons. The maize mutants¹ Tassel-seed 2 (*ts*₂), Tassel-seed 5 (*Ts*₅), Tassel-seed 6 (*Ts*₆), Vestigial glume (*Vg*), Tunicate (*Tu*), *Ramosa-1* (*ra*₁) and Male-sterile 1 (*ms*₁, later shown to be identical to tassel-seed 8 of Nickerson & Dale, 1955) were grown, treated and studied.

MATERIALS AND METHODS

Planting distances and cultural methods employed are the same as those set forth in an earlier account (Nickerson and Embler, 1960). There were generally 2 or 3 lots of seed available for each of the above-listed mutants. Each of the stands of plants resulting from these seed lots was divided into four groups with as nearly equal numbers as possible; all plants in a particular group received the same treatment.

Concentrations of GA chosen were in the range shown by a previous study (Nickerson, 1959) to have a detectable but not drastic effect on field-grown maize plants. The four treatments employed were as follows:

- 1 — distilled water (controls)
- 2 — distilled water with 50 ppm GA

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¹ Thanks are hereby gratefully extended to Dr. Earl B. Patterson, Department of Botany, University of Illinois, Urbana, Illinois, for providing seed from Maize Genetics Cooperation sources for this study.

3 — distilled water with 100 ppm GA

4 — distilled water with 150 ppm GA

Each third day for the duration of treatments one ml. of the appropriate solution containing either distilled water or water plus the above-listed amounts of GA² was applied from a pipette into the apical cavity of each plant. Solutions were freshly made each time, or stored no longer than three days in darkness at 19° C. Planting dates, beginning treatment dates, ending treatment dates, total numbers of plants grown and total amounts of GA applied to each mutant are shown in Table I.

RESULTS

Tassel-seed 2 (*ts*₂). Seed stocks employed had no normal sibs. Because of the extreme general uniformity of plants within each treatment group, measurements were made only on four single treated plants exhibiting the mutant form (Table II). Central spike length was generally decreased with increasing dosage, as were the number of primary tassel branches, the area over which they originated, and the number of ears produced. Peduncle length was about equally decreased by all three dosage levels of GA. Internode number was hardly influenced at all. Plant height showed increase with GA treatment; each group of treated plants in the field was highly uniform in total plant height, but internode diagrams (Fig. 1) show that early-formed internodes were increasingly lengthened by increasing doses of GA, while later-formed ones became much shorter than those of the distilled-water-treated mutant plant. Specimen tassels show a rapid decrease in overall size, but proportions of peduncle length, branch number, spikelet number and caryopsis development remain relatively constant (Plate XII).

Tassel-seed 5 (*Ts*₅). Plants were either normal (+/+) or heterozygous (*Ts*₅/+) in genetic constitution. Figures listed under "M" on Table II are averages for 4 mutant (*Ts*₅/+) plants; figures listed under "C" are measurements for the single control (+/+) plant in that group. Length of central spike was depressed solely by doses of 100 ppm GA in mutant-carrying plants; only slight changes were manifested in normal sibs. Tassel branch numbers fluctuated with no definite pattern in treated mutant-carrying plants; a consistent reduction was noted by all strengths of GA employed on normal sibs. The length of stem over which tassel branches developed was relatively consistent for both mutant-carrying and normal sibs regardless of GA concentration employed. Peduncle length of normal sibs was relatively uniform, but 50 ppm doses of GA tended to shorten this length somewhat in mutant-carrying plants, while 150 ppm doses tended to lengthen peduncles by about the same amount. Internode number increases consistently in mutant-carrying plants with increasing dosage; in normal sibs the number is uniformly increased by all GA levels employed. Ear number is increased in both mutant-carrying plants and normal sibs by doses of 50 ppm GA; further increase in GA dosage level does not decrease ear number in mutant-carrying plants, but drastically does so in normal sibs.

Plant heights of mutant-carrying plants, nearly equal to those of normal sibs

² The GA employed was kindly supplied by Dr. Curt Leben, Agricultural Research Division, Eli Lilly and Company, Greenfield, Indiana.

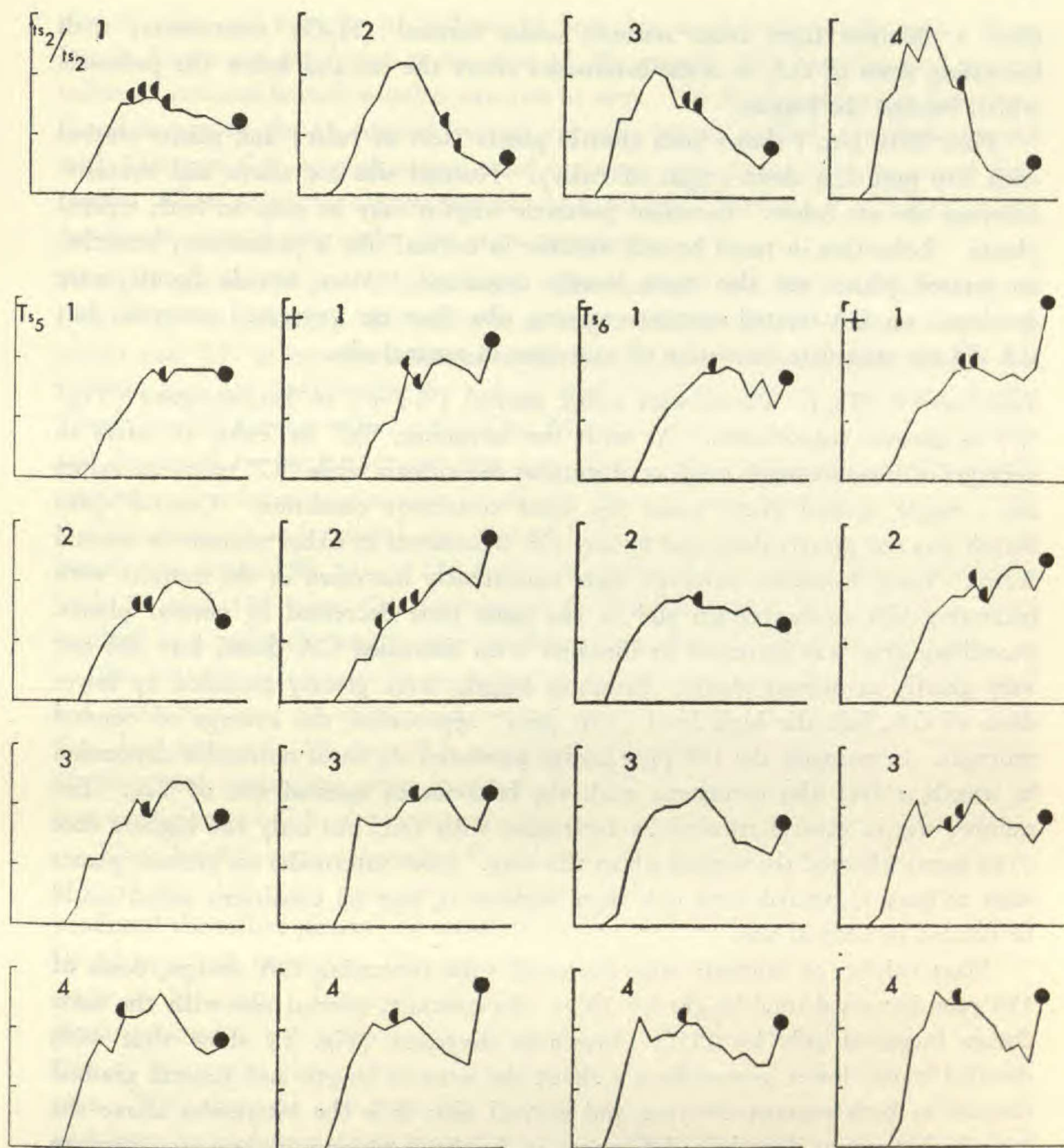


Fig. 1.

Figs. 1-3. Internode diagrams of various maize plants with either normal or mutant conditions showing responses to treatment with GA. Numbers are indicative of treatments, as follows: 1, distilled water; 2, 50 ppm GA; 3, 100 ppm GA; 4, 150 ppm GA. Internode lengths are indicated in 10-cm. units on ordinate; internode number may be determined from the abscissa. These graphs were all plotted from the tassel down, so all tassels (dots) are in the same relative position on each graph. Ears are represented as semicircles.

under control (H_2O) doses, are not as sensitive as those of normal sibs until the GA dosage reaches 150 ppm. Analysis of internode diagrams show that peduncle lengths in normal sibs are as long or longer than the longest lower internodes. The consistent dip below the peduncle and above the ear is present in all cases. With increase in dosage, early-formed internodes become longer. Mutant-carrying plants

show a different form from normals under control (H_2O) treatments; with increasing doses of GA, it is the internodes above the ear and below the peduncle which become the longest.

Plate XIII, No. 1 shows both control plants (left of ruler) and plants treated with 150 ppm GA doses (right of ruler). Normal sibs are above and mutant-carrying sibs are below. Increased peduncle lengths may be seen on both treated plants. Reduction in tassel branch number in normal sibs is prominent; branches on treated plants are also more loosely organized. More female florets were developed on GA-treated mutant-carrying sibs than on untreated controls, but GA did not stimulate formation of caryopses in normal sibs.

Tassel-seed 6 (Ts_6). Plants were either normal (+/+) or heterozygous (Ts_6 /+) in genetic constitution. As with the foregoing, "M" in Table II refers to averages of measurements made on 4 mutant individuals while "C" refers to values for a single normal plant under the same treatment condition. Central spike length was not greatly decreased by any GA treatments in either mutant or normal forms. Tassel branches, however, were consistently increased in the mutant with increasing GA concentration and at the same time decreased in normal plants. Branching area was increased in mutants with increased GA doses, but did not vary greatly in normal plants. Peduncle lengths were greatly modified by lower doses of GA, but the high level (150 ppm) approached the average of control mutants. In normals, the 100 ppm dosage produced the most noticeable depression in length, a fact also consistent with the behavior of normal sibs of Ts_5 . Ear number was in general reduced by treatment with GA, but only the highest dose (150 ppm) affected the normal sib in this way. More internodes on mutant plants seem to have elongated with GA than without it, but no consistent trend could be noticed in normal sibs.

Plant heights of mutants were increased with increasing GA dosage; doses of 150 ppm increased total height by 50%. By contrast, normal sibs with the same dosage increased only by 11%. Internode diagrams (Fig. 1) show that with distilled water, lower internodes are about the same in length and general gradual increase in both mutant-carrying and normal sibs; it is the internodes above the ear which account for their differences in height. 50 ppm treatments seem to stimulate all internodes about equally, except for a reduction in peduncle length of the normal sib. 100 ppm of GA has a greater stimulation of lower internodes but apparently tends to shorten all upper internodes. 150 ppm doses on both mutant-carrying and normal sibs show a marked effect on the early internodes with a peak length reached below the ear; each internode is then shorter up until the peduncle, which although long, does not exceed the longer internode. A comparison between these last curves shows a considerable amount of similarity.

Plate XIII, No. 2 shows tassels from mutant-carrying and normal sibs. Those on the left of the ruler received treatment with distilled water; those on the right with 150 ppm GA. Peduncle growth in mutant-carrying plants is notable, reduc-

tion of silks and increase in stiffness of branches are likewise easily seen. Some female florets are developed at the base of the normal sib's branches and central spike; its reduced branch number can also be seen. No developed kernels have been found in any of the 15 control mutant-carrying tassels studied. In those treated with 150 ppm GA, several normal-sized caryopses were noted in three out of four tassels. These caryopses always were in the same basal locations at which caryopses develop in normal sibs under this same treatment.

Vestigial glume (Vg). Plants were either normal (+/+) or heterozygous (Vg/+). In Table III, "M" refers to average measurements of 4 mutant-carrying plants and "C" to measurements of single normal sibs. Central spike length was reduced but not consistently by GA in both mutant-carrying and normal sibs. Tassel branch number was increased by 50 ppm doses on mutant-carrying plants and decreased by both 100 and 150 ppm doses. On normal sibs, tassel branch number was reduced consistently by all GA doses. Tassel branching area for both mutant-carrying and normal sibs showed little or no response to GA. Peduncle length was reduced by 50 and 150 ppm GA treatments in mutant sibs; in normals, both 50 and 100 ppm GA treatments caused reductions, but 150 ppm doses resulted in a peduncle length close to that of the distilled water-treated plant.

Ear number was generally increased on mutant-carrying plants with increased GA concentration; ear number on normal sibs was increased by doses of 100 ppm GA, but doses of 150 ppm GA completely inhibited ear formation. Numbers of elongated internodes were increased by GA in mutant-carrying sibs by all concentrations of GA; approximately the same results were noted in normal sibs.

Plant heights were adversely affected in both groups by 50 ppm GA doses; in normal sibs, 100 ppm doses produced even shorter plants, while 150 ppm doses produced the tallest plants. In mutant-carrying sibs, an adverse effect is also noted by 50 ppm GA doses, but 100 ppm doses produced a greater average height than doses of 150 ppm. Internode diagrams (Fig. 2) show similar curves for both mutant-carrying and normal sibs. Doses of 50 ppm GA markedly depress elongation of internodes above the ears and do not influence internode length below the ears. With doses of 100 ppm GA early-formed internodes are greatly elongated and later-formed ones even more drastically reduced. Curves for plants which have been subjected to doses of 150 ppm GA show that internodes immediately below sites of ear formation are most greatly stimulated in elongation while those immediately below the peduncles are most strongly inhibited in elongation.

Plate XIV, #1 is of normal sibs (upper tassels) and mutant-carrying sibs (lower tassels) of plants treated with distilled water (left of ruler) and 150 ppm doses of GA (right of ruler). Tassel branch reduction under GA treatment is apparent. Shortening of the mutant-carrying peduncle by GA may also be seen. Production of female caryopses (florets) does not occur in either normal sibs or mutant-carrying plants with this dosage; a very few are developed at the base of the lowermost tassel branch under 100 ppm doses in both mutant-carrying and normal sibs.

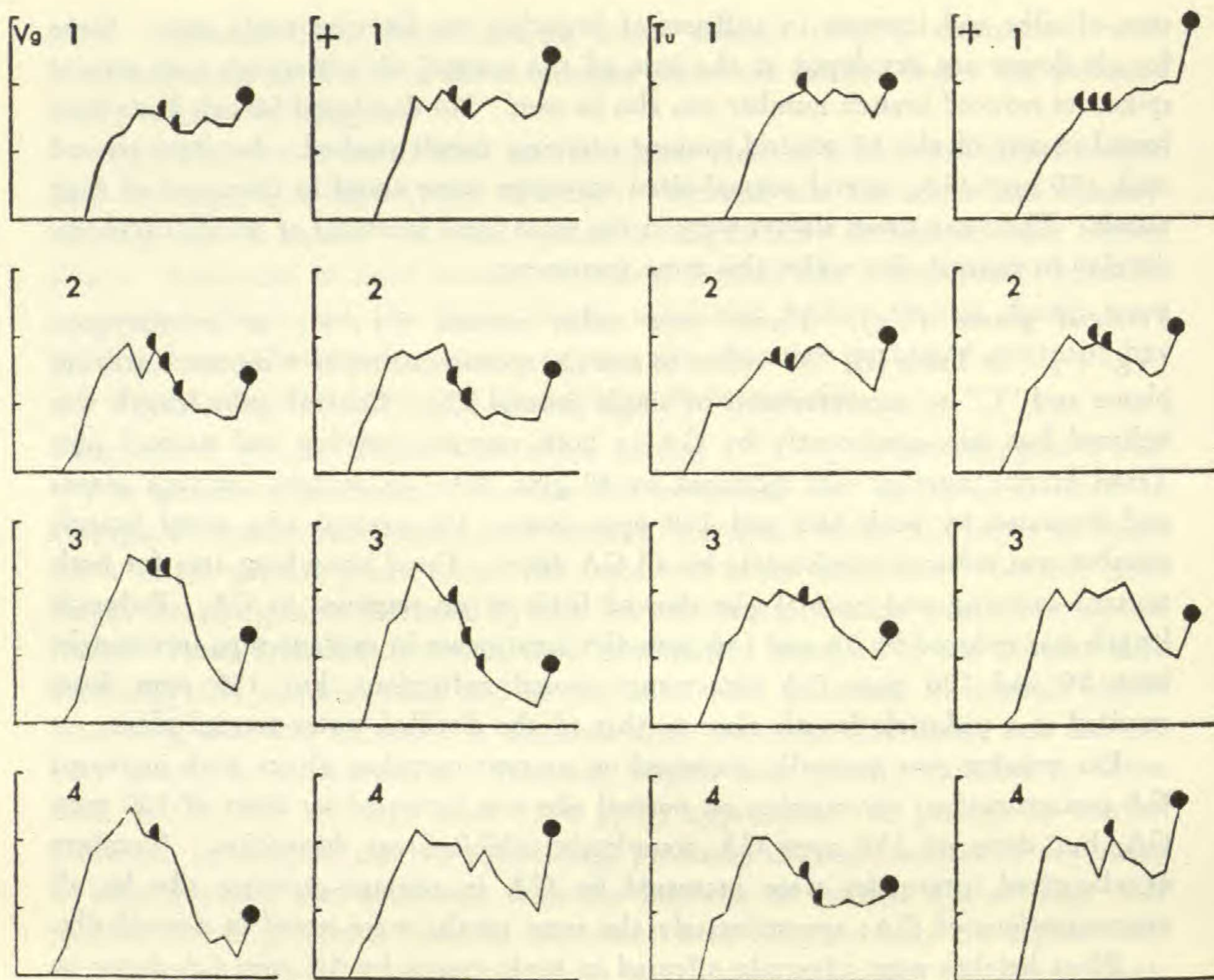


Fig. 2.

Tunicate (*Tu*). Plants were either normal (+/+) or heterozygous (*Tu*/+) in genetic constitution. Column "M" in Table III is based on average measurements of 4 mutant-carrying plants, while column "C" figures are for single normal plants. Central spike length is increased in mutant-carrying sibs by doses of 50 and 100 ppm GA. In normal sibs, no reduction in length is noticed until doses reach 150 ppm; this highest dose also shortens central spike length of mutant-carrying sibs, but not as profoundly. Tassel branch numbers are decreased by about half by all doses of GA in mutant-carrying plants; 50 ppm and 100 ppm doses on normal sibs cause great reduction, but 150 ppm doses seem to have little effect. The length of culm over which branches arise is not changed much on both mutant-carrying and normal sibs by any treatments, except that 50 and 100 ppm doses on normals apparently cause some reduction. These two dose levels likewise cause a reduction of peduncle length in normal sibs. Peduncle length in mutant-carrying plants is noticeably decreased only by doses of 150 ppm GA. Ear number is relatively constant for all mutant-carrying sibs, but increased dosages cause decreases in ear formation on normal plants. Internode number of normal sibs is

actually reduced slightly by doses of 150 ppm GA; this same dosage causes more internodes to elongate in mutant-carrying sibs.

Plant heights of normal sibs are not altered significantly by any GA treatments; increases in heights of mutant-carrying sibs were obtained with doses of 50 and 100 ppm, but 150 ppm treatments produced plants whose average lengths were shorter than those of plants subjected to the lower concentrations. Internode diagrams (Fig. 2) show that while normal sibs treated with distilled water show generally increasing internode lengths from base to peduncle; 50 and 100 ppm GA treatments tend to elongate lower internodes and shorten upper internodes. Doses of 150 ppm GA tend to make all internodes long. In mutant-carrying plants, internodes above the ear tend to remain the same length as in water-treated plants. Doses of 50, 100 and 150 ppm progressively make lower internodes longer and upper internodes shorter.

Plate XIV, #2 shows tassels from normal and mutant-carrying sibs. Those treated with distilled water are left of the ruler; those treated with 150 ppm doses GA are at the right. Normal sibs are uppermost, mutant-carrying sibs are lowermost. Reductions in tassel branch number are apparent. Development of silks and large glumes at bases of branches of mutant-carrying sibs are seen. The shorter peduncle is also prominent.

Ramosa-1 (ra_1). Crosses were made so that plants were either heterozygous ($+/ra_1$) or homozygous (ra_1/ra_1) in genetic constitution. In Table III, column "M" represents average measurements of four homozygous plants; column "C" figures are for single heterozygous plants. Central spike lengths were not greatly altered in either homozygous or heterozygous plants, except for some increases in both plant types under doses of 100 ppm GA. 50 ppm doses of GA reduced tassel branch number in heterozygous but not in homozygous sibs. 100 ppm doses were not as effective on heterozygous sibs as were 50 ppm doses, but on homozygotes, a marked reduction of branching was obtained. 150 ppm doses were as effective as 100 ppm doses on heterozygotes, but on homozygotes a reduction in average branch number of more than 50% resulted. The length of culm over which these branches arise was affected by doses of 150 ppm only. This same dosage increased the length in heterozygous plants and decreased the length in homozygous sibs. The final result in each case was nearly identical, a fact borne out by the two tassels on the right in Plate XV, #1. Average peduncle lengths did not differ with treatment in homozygotes, but with heterozygotes, an apparent reduction under 100 ppm doses and 33% increase under 150 ppm doses was obtained.

Ear number in homozygotes was generally reduced by GA treatments, but ears were still the highly branched forms typical for ra_1 (Nickerson and Dale, 1955). The reduction was greatest with 150 ppm GA doses, but all strengths did cause a decrease. In heterozygotes, all GA treatments caused a consistent amount of reduction. Internode number in homozygotes was apparently increased most by doses of 50 ppm GA; higher concentrations reduced this number, but it remained higher than the average for control (water-treated) plants. 100 ppm doses

affected heterozygotes greatest; a reduction below the number present in controls was noted at the 150 ppm level.

GA increased plant heights of homozygotes in a linear relationship to dosage; with the exception of 150 ppm doses, heterozygotes behaved the same way. Even this latter plant, however, was $\frac{1}{3}$ higher than its sib which received only distilled water. Internode diagrams (Fig. 3) show that the general pattern exhibited by water-treated homozygotes of increasing internode length up to the ear and further increases for each internode above the ear were simply accentuated for all levels of GA dosage employed. Heterozygous sibs show the same basic pattern with water treatments, with 50 ppm doses and, with some deviation, with 150 ppm doses. Doses of 100 ppm, however, apparently caused many of the internodes produced above the ears to be generally shorter (with one glaring exception) than those preceding them.

Plate XV, #1 shows tassels of heterozygous (upright) and homozygous plants (inverted). The two on the left were treated with distilled water; those on the right with 150 ppm GA. Note reduction in tassel branch numbers and increase in peduncle lengths. Female caryopses were nearly non-existent, on either hetero- or homozygotes.

The strong resemblance of both treated homozygous and heterozygous tassels to control tassels of $+/+$ plants in Plate XIV should be noted.

Male-sterile 1 (ms_1). Plants were either heterozygous ($+/ms_1$) or homozygous (ms_1/ms_1) in genetic constitution. In Table III, "M" columns are average measurements of four mutant-carrying plants and "C" columns are measurements for single heterozygous normal sibs. Central spike lengths of heterozygous plants were decreased by increasing doses of GA; treatments of 150 ppm caused a 27% decrease. Central spike lengths in homozygous sibs were stimulated by doses of 50 ppm GA, but 100 ppm and 150 ppm doses caused only slight variations from lengths attained by control (water-treated) plants. Tassel branch number, tassel branch area and peduncle length were generally unaffected in both homozygous and heterozygous plants by all GA dose levels; the single deviation in this pattern was the heterozygote under 150 ppm doses, where a 50% reduction in branch number was obtained. Ear number was not reduced in homozygotes except under doses of 100 ppm GA; heterozygotes showed an increase over the control under doses of 50 ppm GA but with higher doses, ear number remained unchanged from that of the control plant.

Internode number of heterozygotes seemed to be increased slightly by 50 and 100 ppm doses. Homozygotes showed a definite increase in number of measurable internodes over control plants with all GA treatment levels.

Plant heights of homozygotes were increased by 50 and 100 ppm doses, but 150 ppm doses did not increase them further. Heterozygotes were relatively unchanged by all GA levels except 150 ppm which caused about a 10% increase in height. Internode diagrams (Fig. 3) show that heterozygotes have a series of internodes that increase rather rapidly and then form a relatively flat plateau with

a slight increase in the peduncle. 50 ppm doses of GA affect later-formed internodes so as to give a series of continually longer internodes from base to tassel. 100 ppm doses increased earlier internode lengths over those shown in controls. 150 ppm doses exaggerated early internode lengths and shortened later ones up to the peduncle, which is about as long as that of the control plant. Curves for homozygotes carrying the mutant show strong similarity in control plants to heterozygotes. 50 ppm doses show no marked changes, but 100 ppm doses tend to accentuate lengths of early internodes and shorten lengths of later-formed ones. This trend is even more pronounced under doses of 150 ppm. The general curve produced is quite similar to that produced by the heterozygote under similar treatment.

Plate XV, #2 shows tassels from heterozygous (upper) and homozygous (lower) plants. Two are from plants treated with distilled water (left of ruler) and two from plants treated with 150 ppm GA (right of ruler). The general reduction in tassel branch number and wider spacing of spikelets on branches is apparent. However, no pollen was shed by homozygotes treated with GA. Three female caryopses with silks were developed at the base of the lowest branch of one mutant-carrying tassel in the five which were collected. Their development in other tassels not harvested was just as scarce.

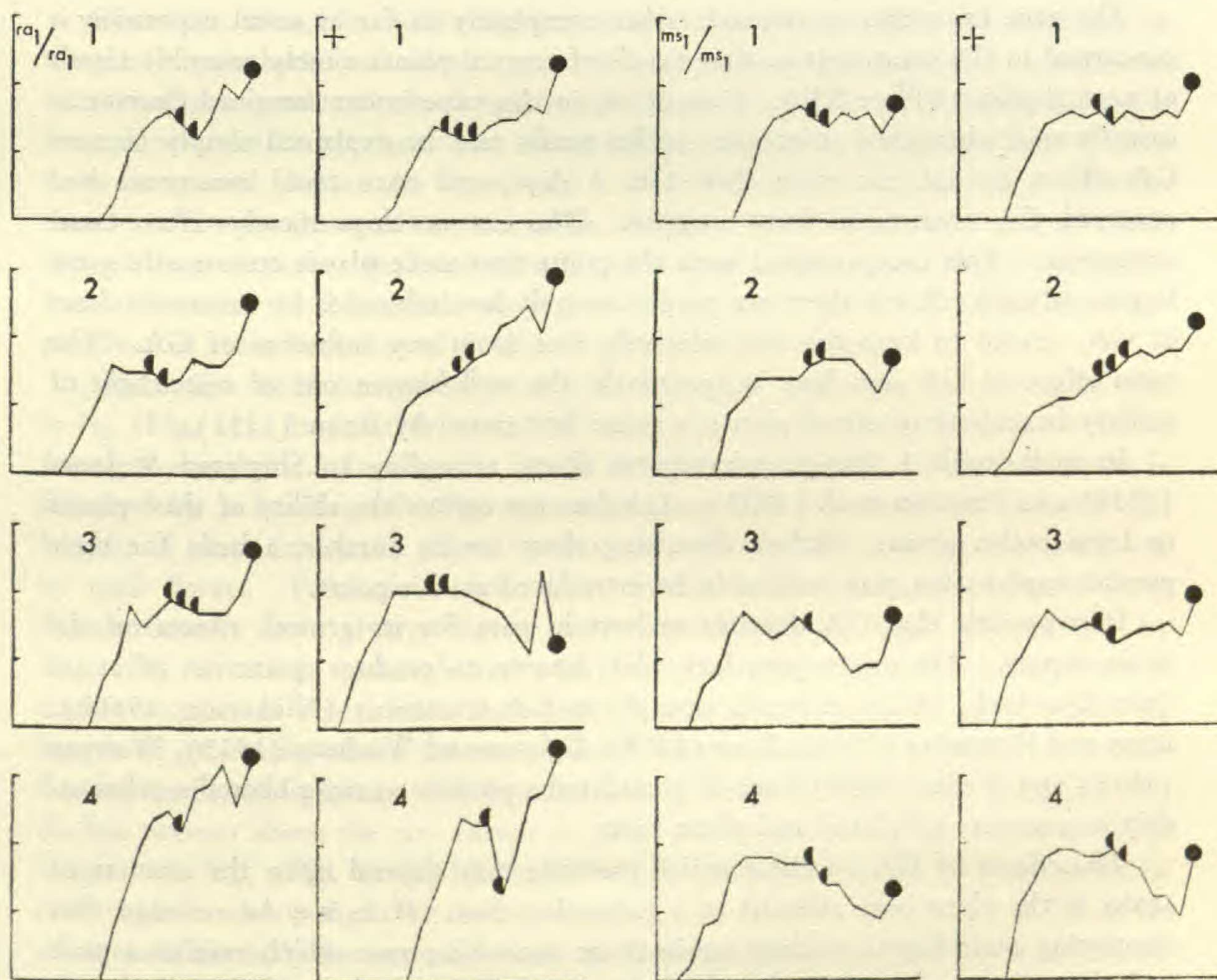


Fig. 3.

DISCUSSION AND CONCLUSIONS

Nickerson and Dale (1955) described certain morphological characters of sixteen tassel mutants. Some of these have been subjected to treatments with GA; it is planned to treat the remainder during the 1960 growing season.

Plants with genotype ts_2/ts_2 showed no lessening of the gene expression under treatment with GA, but tassels were smaller with increased doses. Expression of Ts_5 was essentially the same under GA treatment. The gene Ts_6 showed several changes in many measurements under GA treatment; resemblances of the tassel in Plate XIV, #2 to untreated ts_4 (Nickerson and Dale, Plate 24, Fig. 2) is remarkable. This gene, however, still is not modified to produce a "normal"-looking or standard tassel under GA treatment.

The genes Vg and Tu are somewhat opposite in their effects on glume growth. GA reduces their expressions somewhat, so that treated plants have many more normal-appearing glumes than untreated plants. GA-treated Vg and Tu tassels, however, did not produce much pollen. This male-sterility effect was earlier noted on normal maize plants treated with GA (Nelson & Rossman, 1958; Nickerson, 1959). Female caryopses were regularly produced in tassels with each of these genes under GA treatment.

The gene ra_1 seems to respond rather completely as far as tassel expression is concerned to GA treatment so that tassels of treated plants closely resemble tassels of normal plants (Plate XV). Ears of ra_1 in this experiment remained characteristically multi-branched structures. This result may be explained simply because GA effects do not last more than 2 or 3 days, and once tassel emergence had occurred GA treatments were stopped. The ear develops mostly after tassel emergence. This fact, coupled with the point that since plants continually grew larger and each cell was therefore proportionately less influenced by successive doses of GA, tended to keep the ears relatively free from any influence of GA. The main effect of GA seen here is apparently the well-known one of restriction of axillary branching in intact plants, a point first noted by Brian (1957).

In male-sterile 1 (ms_1), microspores abort, according to Singleton & Jones (1930) and Emerson *et al.* (1935). GA does not restore the ability of these plants to form pollen grains. Before discussing these results further, a basis for their possible explanation may profitably be introduced at this point.

It is possible that GA depends at least in part for its growth effects on the auxin supply. The maize gene *lazy* (la), known to produce quantities of auxin (van Overbeek, 1938) responds strongly to GA treatment (Nickerson, 1960b). Brian and Hemming (1958), Kuse (1958), Galston and Warburg (1959), Wareing (1958) and Weijer (1959) have all postulated a positive auxin-gibberellin relationship in a variety of plants and plant parts.

The effects of GA on these maize mutants may depend upon the amount of auxin in the plant part affected at a particular time. If it may be assumed that developing male florets produce auxin in an increasing rate which reaches a peak and then drops off rapidly shortly before anthesis, and that developing female

florets produce far greater quantities much quicker, and for a longer time but later in the life of the plant, then one could postulate the following relationship. As the tassel of a normal (+/+) plant begins its development, the peduncle receives elongation stimulus (auxin) in greatest quantity first. However, the amount of auxin produced by the tassel quickly reaches the level above which stem elongation ceases. Thus the peduncle matures early (Murdy, 1960), and the lowermost internodes elongate and mature from the base up as the auxin concentration from above rapidly increases and then decreases. The ear-shoot (an axillary bud) is stimulated by the high point of auxin concentration reached; it then begins to develop and forms silks rapidly. About the time silks are extruded, the auxin supply from the tassel diminishes toward zero. Under the influence of a diminishing auxin supply, the internodes below the peduncle but above the ear, heretofore inhibited by a high auxin concentration, finish their elongation and mature. Brace roots develop at the lower end of the culm, again as the auxin supply falls below the optimum for stem growth. Shortly thereafter, the pollinated ear produces quantities of auxin which quickly results in an excess over optimum for either stem or bud development; the internodes of the ear shoot or shank thus do *not* elongate. In many forms, the shank never fully matures, producing a structure which bends easily under the weight of the developed ear.

There are, then, the following general patterns of growth which conform to the above hypothesis concerning auxin concentrations and GA effects. Tassel-seed 2, normally a producer of quantities of female caryopses in the tassel, has its lower internodes longer than those of normal plants and its upper ones shorter than those of normal plants. In Tassel-seed 5, the first third of tassel florets differentiated are female (bases of central spikes and lower tassel branches) and all later-formed ones are male. In Tassel-seed 6, the reverse is true; the first third of spikelets in the same tassel locations are male and all outer (and later) ones are much-proliferated short branches of poorly-developed female florets.

Gibberellic Acid treatment accelerates both the early rise and the later dip in ts_2 (Fig. 1). Presumably auxin concentration rapidly reached inhibitory levels for stem elongation. In Ts_5 , the rise in lengths of internodes in control plants is followed by a leveling-off (Fig. 1); subsequent GA treatments accentuate the lengths of those internodes above the ear, formed when most auxin was produced by male florets. Peduncle lengths (here formed under amounts of auxin from female florets) were always shorter than these elongated upper internodes. In Ts_6 , (Fig. 1) a long peduncle and a steep rise in early internode length (formed under amounts of auxin from male florets) was always followed by a decline in length of internodes above the ear (formed under amounts of auxin from female florets) in control plants. GA accentuates the early rise but does not affect the decline pattern above the ears except to make all internodes slightly but uniformly longer. In Vg , (Fig. 2) an internode length is reached rapidly which decreases only slightly with a slight increase in the peduncle length. The effect of GA is to accentuate the early increase and cause marked declines in internode lengths above

the ear, with the earlier-formed peduncle length showing a final strong increase. Since the stamens of *Vg* dry out and die before anthesis, the late supply of tassel auxin is presumably cut off. *Tu* (Fig. 2) follows the same pattern but GA effects are less pronounced. *Ramosa-1* (*ra*₁, Fig. 3) has an internode pattern of general increase in length from base to tip; here all florets remain male, but they are quite numerous and shed pollen over a much longer period than do normal plants. GA treatment accentuates this pattern but preserves its general form.

In *ms*₁ (Fig. 3) a sharp initial increase in internode length is followed by leveling-off with only a slight dip before the peduncle. GA accentuates both the early rise and the late dip. The fact that microspores form but then degenerate before anthesis with possible consequent severe decrease in tassel auxin production would account for the GA behavior if it depended upon auxin concentration for its elongation effects.

Confirmation of many points in the above discussion must occur before it will satisfy critical investigators. It may, however, be suggested that not only does GA apparently depend upon the presence of auxin for its elongation effects, but it also depends upon the particular concentration of auxin (and GA) available in the elongating cells. A possible point in favor of this hypothesis is that it seemingly explains the effect of GA upon the dwarf gene *nana* (*na*₁); Phinney (1956) reported it as "not responding to GA treatments". Van Overbeek (1935) had previously shown that although *nana* made even more than normal amounts of auxin, the material was destroyed before it diffused down the culm. If there were no auxin, then GA, which presumably depends upon its presence for at least part of its effects, would cause no such effects. There are some facets of GA effects not explained by this proposal, but elongation effects in maize may reasonably be regarded in this manner.

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LITERATURE CITED

- Brian, P. W. (1957). The effects of some microbial metabolic products on plant growth. Soc. Exptl. Biol. Symposium XI. Biological Action of Growth substances: 166-182. Cambridge Univ. Press.
- , and Hemming, H. G. (1958). Complementary action of GA and auxins in Pea internode extension. *Ann. Bot., N. S.* 22:1-17.
- Emerson, R. A., Beadle, G. W. and Fraser, A. C. (1935). A summary of linkage studies in maize. Cornell Univ. Agri. Expt. Sta. Memoirs 180:1-83.
- Galston, A. W. and Warburg, H. (1959). An analysis of auxin-gibberellin interaction in Pea stem tissue. *Plant Physiology* 34:16-32.
- Kuse, G. (1958). Necessity of auxin for growth effect of Gibberellin. *Bot. Mag. Tokyo* 71:151-159.
- Murdy, W. H. (1960). The strengthening system in the stem of maize. *Ann. Mo. Bot. Gard.* 47: 205-226.
- Nelson, P. and Rossman, E. C. (1958). Gibberellin-induced male sterility in inbred maize. *Science* 127:1500-1501.

- Nickerson, N. H. (1959). Sustained treatment with Gibberellic acid of five different kinds of maize. *Ann. Mo. Bot. Gard.* 46:19-37.
- , (1960a). Sustained treatment with Gibberellic acid of maize plants carrying one of the dominant genes Corn-grass and Teopod. *Amer Jour. Bot.* (in press).
- , (1960b). Studies involving sustained treatment of maize with Gibberellic acid III: Responses of *Zea mays* plants carrying the gene "lazy". *Amer. Midl. Nat.* (in press).
- , and Dale, E. E. (1955). Tassel modification in *Zea mays*. *Ann. Mo. Bot. Gard.* 42: 195-212.
- , and Embler, T. N. (1960). Studies involving sustained treatment of maize with Gibberellic acid I: Further notes on responses of races. *Ann. Mo. Bot. Gard.* 47:227-242.
- Phinney, B. O. (1956). Growth response of single-gene dwarf mutants in maize to gibberellic acid. *Proc. Nat. Acad. Sci.* 42:185-189.
- Singleton, W. R. and Jones, D. F. (1930). Heritable characters in maize. XXXV. *Jour. Hered.* 21: 266-268.
- van Overbeek, J. (1935). The growth hormone and the dwarf type of growth in corn. *Proc. Nat. Acad. Sci. U. S.* 35:292-299.
- , (1938). "Laziness" in maize due to abnormal distribution of growth hormone. *Jour. Heredity* 29:339-341.
- Wareing, P. F. (1958). Interaction between IAA and GA in cambial activity. *Nature* 181:1744-45.
- Weijer, J. (1959). Interaction of Gibberellic acid and IAA in *Impatiens*. *Science* 129:896-897.

TABLE I

PLANTING AND TREATMENT DATA OF SEVEN MAIZE MUTANTS

Mutant	Planting Date (1959)	Date of first GA treatment	Total number of plants treated	Date of last GA treatment	Total number of treatments	Total Amounts of GA applied in micrograms		
						50 μ g per dose	100 μ g per dose	150 μ g per dose
ts ₂	15 June	6 July 1959	86	14 August 1959	fourteen	700 μ g	1400 μ g	2100 μ g
Ts ₅	16 June		104					
Ts ₆	16 June		96					
Vg	14 June		107					
Tu	14 June		126					
ra ₁	12 June		87					
ms ₁	15 June		117	26 August	18	900 μ g	1800 μ g	2700 μ g

TABLE II
RESULTS OF GA TREATMENT ON CERTAIN MEASUREMENTS OF THREE MAIZE TASSEL-SEED GENOTYPES AND THEIR NORMAL SIBS

Genotype	Dosage of GA in micro- grams	Length of central spike (cm.)		Number of primary tassel branches		Length of tassel branching area (cm.)		Peduncle length (cm.)		Plant height (cm.)		Number of internodes		Number of ears	
		M	C	M	C	M	C	M	C	M	C	M	C	M	C
M = ts_2/ts_2 (single plant measure- ments)	0	27		15		10		11		171		14		4	
	50	16		12		8		5		182		15		2	
	100	20		8		8		7		182		15		2	
	150	12		13		5		5		203		15		1	
M = $Ts_5/+$ (av. of 4) C = $+/+$ (single plant measure- ments)	0	26.5	26	11	21	8.5	13	15	22	168	172	11.5	11	1.2	2
	50	30.5	30	6	14	7	14	11.5	26	177	202	12.5	13	2	4
	100	18	28	12	14	10.5	13	14.2	21	205	236	12.5	13	1.7	1
	150	27	24	8	14	7.5	15	18.5	26	240	231	13	13	2.2	1
M = $Ts_6/+$ (av. of 4) C = $+/+$ (single plant measure- ments)	0	12	35	15	14	10.2	13	25	29	167	225	13	14	1.2	2
	50	9.5	27	16	13	11	13	12	23	202	226	15	13	0.5	2
	100	9.5	32	18	8	15	10	14	17	217	241	15.5	15	0.5	2
	150	11	27	21	9	15.5	16	21	24	240	255	15	13	0.7	1

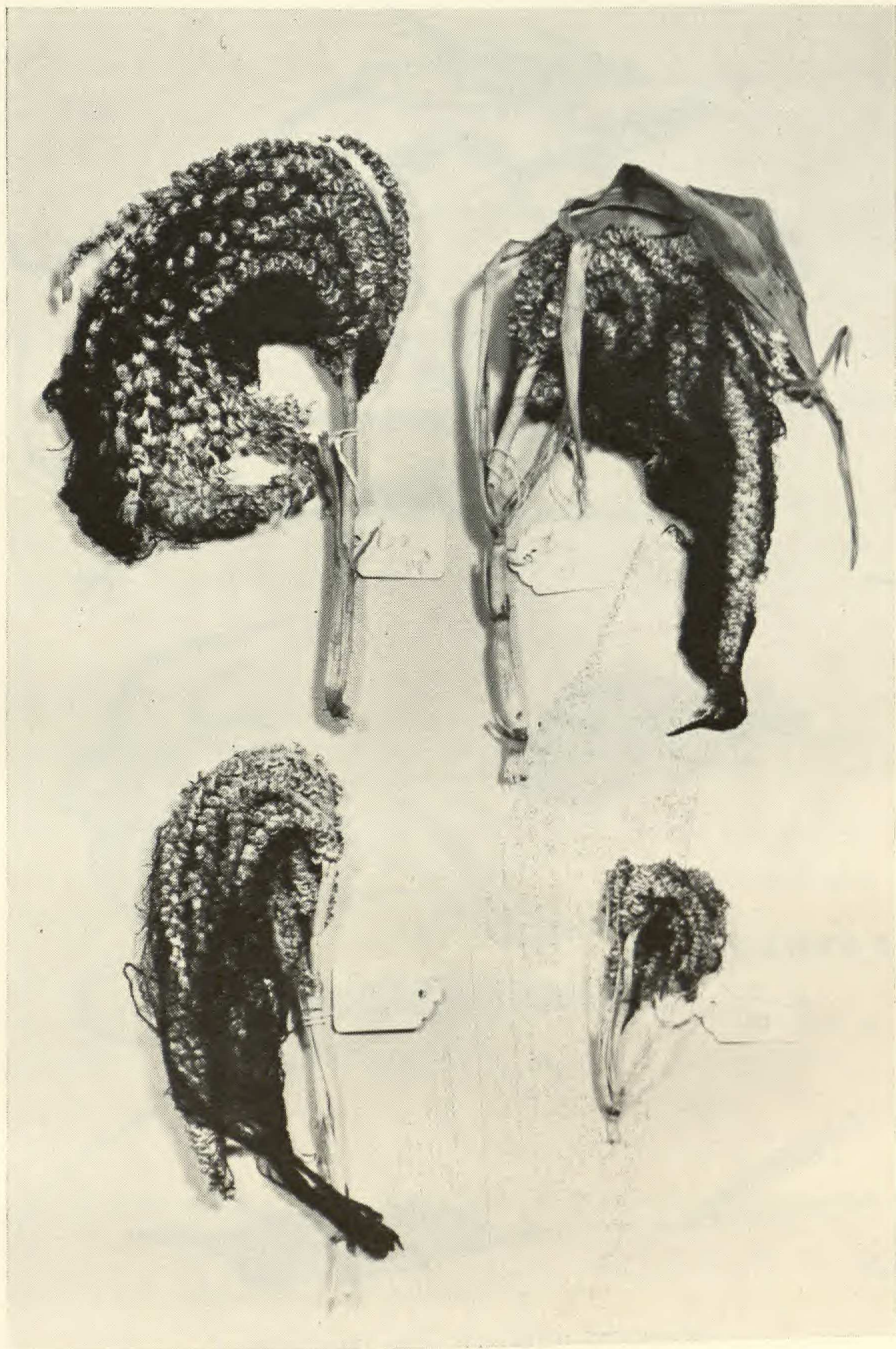
TABLE III
RESULTS OF GA TREATMENT ON CERTAIN MEASUREMENTS OF FOUR MAIZE TASSEL GENOTYPES AND THEIR NORMAL SIBS

Genotype	Dosage of GA in micro-grams	Length of central spike (cm.)		Number of primary tassel branches		Length of tassel branching area (cm.)		Peduncle length (cm.)		Plant height (cm.)		Number of internodes		Number of ears	
		M	C	M	C	M	C	M	C	M	C	M	C	M	C
M = Vg/+ (av. of 4) C = +/+ (single plant measurements)	0	28	31	14	15	10	12	17.5	23	178	207	12.5	13	1.2	2
	50	14.5	28	18	9	10	9	13	14	155	185	14	15	2.2	2
	100	23.5	24	9	10	11	10	16	8	238	168	14	14	2	3
	150	15	25	10	10	12	13	9	21	218	234	15	15	4	0
M = Tu/+ (av. of 4) C = +/+ (single plant measurements)	0	22.5	28	21	14	13	14	17	28	176	208	11.5	13	1.2	3
	50	27	28	10	5	12	9	18	20	196	204	14	13	1.7	2
	100	28	30	13	6	13	9	14	15	203	211	13.5	14	1.2	1
	150	15	9	12	14	10	14	12	25	190	216	13	12	1.2	1
M = ra ₁ /ra ₁ (av. of 4) C = +/ra ₁ (single plant measurements)	0	11	21	64	18	31	13	23	22	155	170	11	13	2.7	3
	50	9	28	63	10	32	12	23	28	196	222	13	13	1.7	2
	100	15	30	39	14	30	10	24	11	213	256	12	15	1.7	2
	150	11	25	25	13	17	20	25	33	236	229	11.5	11	1.2	2
M = ms ₁ /ms ₁ (av. of 4) C = +/ms ₁ (single plant measurements)	0	15	22	10	14	7	9	15	19	166	202	12.5	14	1.7	2
	50	21	21	8	16	9	10	14	21	181	200	14.5	15	1.7	3
	100	13	20	11	14	8	12	15	18	199	205	15	15	1	2
	150	17	16	8	7	8	9	13	17	199	219	15	14	1.7	2

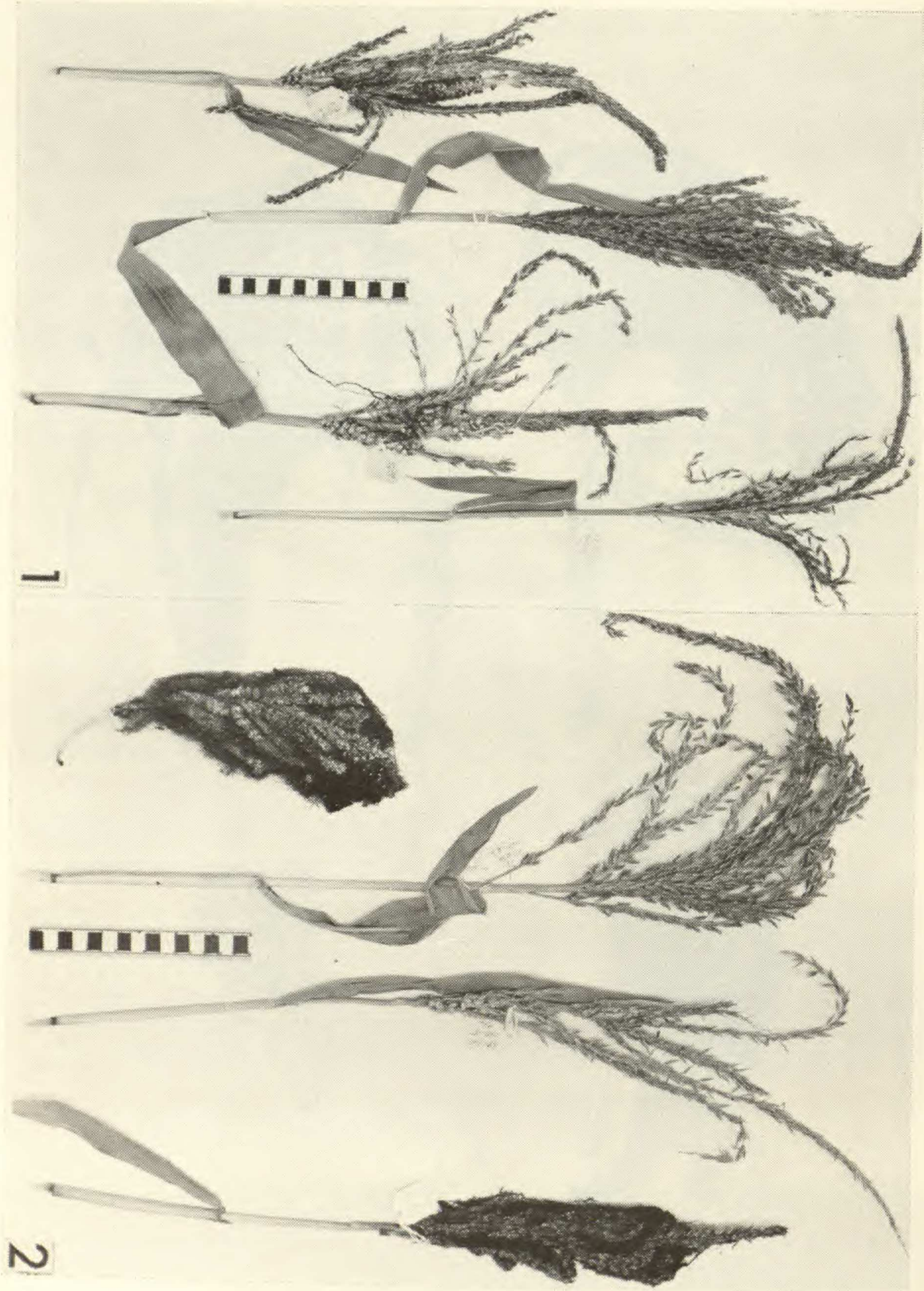
EXPLANATION OF PLATE

PLATE XII

Tassels of ts_2/ts_2 maize plants treated with, from left to right; top row, water and doses of 50 ppm GA; bottom row, doses of 100 and 150 ppm GA.



NICKERSON—GIBERELIC ACID TREATMENT II



NICKERSON—GIBERELIC ACID TREATMENT II

EXPLANATION OF PLATE

PLATE XIII

Tassels of $Ts_5/+$ (lower) and $+/+$ (1) and $Ts_6/+$ (extreme left and right) and $+/+$ (2) maize plants. Those left of ruler were treated with distilled water; those on right with doses of 150 ppm GA.